

30. DESCRIPTION AND DISCUSSION OF MATERIAL BEARING ON MIMICRY IN SOUTH AFRICAN RHOPALOCERA COLLECTED BY GUY A. K. MARSHALL, AND THE RECORD OF OBSERVATIONS MADE BY HIM. (E. B. P.)

The splendid material which is described and discussed below has gradually accumulated as the result of Mr. Marshall's kind and generous response to my desire for specimens for the Hope Department illustrating the fact that mimetic species and their models, and the members of large convergent or synaposematic groups, not only inhabit the same areas but fly together at the same time. The study of this material naturally led to conclusions and suggestions which it is hoped possess a general interest in relation to the doctrine of evolution and the important part which mimicry plays in it, as one of the chief evidences of the operation of natural selection. These more general discussions are placed under separate headings immediately after the groups whose study gave rise to them.

The last sub-section is placed under Mr. Marshall's name, being quoted *in extenso* from his letters.

A. *Black-and-White Amauris-like Group.*

The central model for the group described below is probably *Amauris ochlea*, but it was not captured on March 27, 1897, when five convergent individuals were taken at Malvern, near Durban, Natal. The group as captured is as follows:—

Planema aganice ♂.

„ *esbria* ♀, var. with white markings.

Neptis agatha ♂.

2 *Nyctemera leuconoë*.

The male *Planema aganice* is but an imperfect member of the group, the lighter markings being buff instead of white, as in the female. We thus find that the latter sex forms closer synaposematic resemblances than the male, when the two sexes differ. It is probable that this relationship between male and female will be found to be generally true of Müllerian mimics in which the sexes exhibit different degrees of likeness to the type of some group characterized by Common Warning Colours. Furthermore, the culmination is often reached in Müllerian

mimicry, just as it is in Batesian where it has long been recognized, in species of which the female enters into a more or less well-marked membership of a group towards which the male has made no apparent approximation. Numerous examples will be found in the present memoir.

This interesting similarity between Müllerian and Batesian mimicry was probably unrecognized until 1894, when it was discovered by F. A. Dixey,* because of the fact that in the first-known examples of Müllerian mimicry in tropical America, which are the most wonderful instances in the world, the convergent pairs and groups contributed by the *Heliconinæ* and *Ithomiinæ* and by different genera within each of these sub-families, are made up of species with males and females which are superficially alike.

Now, however, that the principle has been recognized by Dixey in many Neotropical Müllerian mimics with differing sexes and here in many Ethiopian, the explanation is doubtless the same as that suggested by Wallace (Trans. Linn. Soc. xxv, Pt. I, 1865) in the case of Batesian mimics, viz. the great importance for the species that the female, with her slower flight and the necessity to pause and lay her eggs, should gain to the full the advantages of that extra advertisement of warning coloration which is conferred by membership in a synaposematic group. This is the interpretation offered by Dixey in his 1894 memoir (q. v.).

Neptis agatha exhibits in an interesting manner that concentration of white markings into four large patches, one upon each wing (save that the fore-wing is invaded by a small portion of the hind-wing patch), and that disappearance of the other bars and markings, except for traces on the under-side, which are characteristic of many Ethiopian species of this genus, and doubtless indicate a synaposematic approach to the black-and-white species of *Amauris* and *Planema* of the Region.

It is too wide a subject to introduce into the present memoir, but I cannot forbear to allude to the evident synaposematic sensitiveness of the genus *Neptis*, leading it to form associations with local conspicuous Rhopalocera. Among the most beautiful of these are *N. venilia* and *N. lactaria*, which resemble the remarkable Danaine genus *Hamadryas*, especially upon the under-side. Again, the

* Trans. Ent. Soc. Lond., 1894, p. 298, note; 1896, pp. 70, 71; 1897, pp. 319, 326-328, 330.

likeness to *Athyma* and *Limnitis* must have struck every naturalist who has looked through the drawers of a tolerably large collection. Col. Swinhoe has recently called my attention to a *Euplaea*-like *Neptis* from China, *N. imitans*.

The resemblance of the genus *Neptidopsis* to *Neptis* seems, on the other hand, to have been due to mimetic approach on the part of the former towards the type set by the latter.

The Hyspid moth *Nyctemera leuconoë* seems to have independently adopted the same aposematic scheme of colouring as the genus *Amauris*, the only change in the direction of the latter dominant type being a slight broadening of the white bar crossing the fore-wings, a broadening which is at once recognizable when this and other African species of the moth are compared with their nearest Oriental allies. The conspicuous and almost certainly specially-protected *Hypsidæ* strongly tend to enter into synaposematic association with other specially-defended forms in various parts of the world. Thus one species approximates towards *Hamadryas*, while, in tropical America, the smaller forms become transparent and resemble the smaller *Ithomiinæ*, while the larger (*Pericopsis*) possess the warning coloration of species of *Melinæa* and *Heliconius*.

B. *Limnas chrysippus*-like Groups.

The first of these groups was captured on March 6, 1897, at Malvern, Natal. It consists of the eight following individuals:—

Limnas chrysippus ♂.

" " ♀, var. *alcippoides*.

Hypolimnas misippus ♀, with pale hind-wings like the last-named insect.

H. misippus ♀, var. *inaria*.

Planema eschria ♀, *chrysippus*-like type-form with white sub-apical bar to fore-wings and reddish-brown black-bordered hind-wings, the ground-colour extending on to the fore-wings.

Acræa euceloni ♂.

A. serena, var. *buxtoni*, ♀.

A. doubledayi ♂.

The latter individual, being a male, is not really a member of the group, inasmuch as it lacks the oblique

sub-apical white bar present in the female of typical *doubledayi*. The presence of the male indicates, however, that the female flies with the other members of this *chrysippus*-like group, of which it forms an imperfect and outlying constituent. The male of *serena* also does not resemble *chrysippus*, while the female is an even more imperfect Müllerian mimic than the female of *doubledayi*. Nevertheless such cases are of the highest interest, inasmuch as they enable us to understand how mimicry arose in species which now exhibit a startling likeness. *A. eucedon*, one of the most perfect Müllerian mimics of *chrysippus*, presents an equally close approximation in male and female.

The fact that the female of *P. esebria* should present two well-marked varieties, one of which falls into a black-and-white group convergent round the species *Amauris*, while the other, the type-form, enters the combination which surrounds *L. chrysippus*, recalls a principle already well known and probably correctly understood in the case of Batesian mimicry. When an abundant well-protected *Acræa* thus approximates to two very different Danaine patterns it is obvious that we are not necessarily driven to a Batesian interpretation of the forms of the female *Papilio cenea*, which approximate to the appearance of *Amauris echeria* as well as to the two other Danaine types alluded to above. The enemies of *chrysippus* and the species of *Amauris* are certainly not precisely the same, and it may well be an advantage to a Müllerian mimic to secure that increased protection from insect-eating enemies which is conferred by belonging to two or more groups.

Furthermore, the Planema has come to resemble the Danaine and not the Danaines the Planema, and this probably indicates that the Danaine is on the whole the less attacked and the better known. It is probably of advantage to the whole group that the Danaine which set the pattern should still be the dominant member of the assemblage of which it is the centre. This dominance is favoured by the individuals of an abundant species joining two or more groups instead of throwing the whole of their number into a single one. In the case of Batesian mimicry, where the mimics are comparatively palatable and would be freely eaten if recognized, the advantage of this di- or trimorphism and the likeness to two or three models is even more obvious.

A second group of the same type was captured in the same locality on March 30, 1897, and consists of six individuals:—

L. chrysippus ♀.

H. misippus ♀, a pale patch in the centre of each hind-wing.

P. esebria ♂, buff sub-apical bar to fore-wing.

A. encedon ♂.

A. serena, var. *buxtoni* ♀.

A. petraea ♀.

The lack of correspondence between the varieties of the females of *H. misippus* and those of the central member of the group is well seen in these two sets. Thus one of the three females is the *inaria* form, although the *klugii* var. of *chrysippus* is almost unknown in S. Africa, while the other two suggest the appearance of the *alceipoides* var., which does indeed occur not uncommonly, but is not nearly so abundant as typical *chrysippus*. The female of *A. petraea* is another outlying member of the group, while the male is altogether outside it.

A third group, captured by Mr. Marshall at Salisbury on April 10, 1898, contains these species:—

L. chrysippus ♀ }
H. misippus ♀ } all typical forms.
 2 *A. encedon* ♂ }

A fourth group captured at the same locality on April 9, 1899, contains:—

2 *L. chrysippus* ♂, ♀ (Plate XIV, figs. 1, 1a).
 2 *Mimacræa marshalli* ♂ (Plate XIV, figs. 2, 2a).

This beautiful Lycaenid mimic presents in some respects a closer approximation to *Aeræa encedon* (Plate XIV, figs. 3, 3a) than to *L. chrysippus*, the primary model of both. Thus the character and contour of the sub-apical white bar of the fore-wing suggests that of the *Aeræa* rather than the *Danaïde*. In the two former the bar is more continuous, in the latter more obviously broken into discontinuous spots, attended by outlying smaller spots. Another far more important similarity between Lycaenid and *Aeræa* is brought about by the numerous conspicuous black spots which in both are scattered over the basal part of the under-side of the hind-wing. In other respects the

under-side of the Lycænid presents a much closer approximation to the Danaine than does the Acraea. In well-marked individuals there are fourteen of these spots in the Lycænid, nineteen in the Acraea. In place of these, the Danaine model possesses, in addition to the marginal white-marked spots and a single spot at the extreme base of the wing, only a row of three spots on the outer boundary of the cell in the female, with an additional white-centred black patch, marking the scent-pouch, in the male. The three spots along the outer margin of the cell are encircled with white, as are all the spots in the Lycænid; while the veins of the under-side of the hind-wing in both are more or less emphasized with white. In these minor but distinct points the Lycænid approximates to the Danaine and not to the Acraea; and furthermore in the fact that the black spots of the under-side of the hind-wing are hardly visible on the upper-side of the Lycænid, while all except the basal ones are as distinct upon the upper- as upon the under-side of the Acraea. In the Danaine they are very distinct although much smaller on the upper-side, but as there are only three in the female and four in the male, the Acraea is in this respect much further from the other two than they are from each other, its distance being still further increased by a few (4—6) large conspicuous black spots on the ground-colour of the basal half of both surfaces of the upper wing. It is noteworthy that these points of divergence on the part of *A. encedon* are characters which it shares with a large number of related species. All the points mentioned above can be well seen in the six upper figures of Plate XIV, which should be compared with the six corresponding figures on Plate XV, showing the prevalent form of the Danaine model and its Acraeine and Lycænid mimics much further north in British East Africa.

In the dark shade of the brown ground-colour the Acraea is much nearer to the Danaine as developed in S. Africa than the Lycænid, and upon the wing the black spots would probably make the Acraea appear still darker. The bright fulvous tint of *M. marshalli* is more of the shade of the Oriental specimens of *chrysippus*. This relationship appears to exist between many of the other African Müllerian and Batesian mimics of *L. chrysippus* and their model, and suggests that the Oriental bright shade is ancestral, although the Oriental intrusion is comparatively

modern, as proved by the relatively small amount of mimicry, and that little very imperfect, in species peculiar to the Region. The fact that the bright Oriental shade still persists in many of the specimens of *chrysippus* from the north-east and probably other parts of Africa, supports the same conclusion.

Mr. Roland Trimen points out that the *Mimacræa* also resembles the female of the type-form of *Planema esebria* (Trans. Ent. Soc. Lond., 1898, p. 15).

Mr. Marshall gives the following account (1902) of the habits of this interesting insect:—"In its general habits *Mimacræa marshalli*, Trim., like *Acræa encedon*, is essentially a woodland (but not a forest) insect, and shows a marked fear of venturing out into open country. *Limnas chrysippus*, on the other hand, frequents both open and woodland stations. When quite undisturbed it flits about in a limited area of the bush with a slow flight exactly resembling that of *L. chrysippus* (see also pp. 481, 482), but when alarmed it is capable of flying with considerable speed, and dodges with great dexterity. When hard pressed it will occasionally rise right over the tops of the trees, descending into the bush again further on. But its usual method of escape is by dodging in and out among the tree-trunks, then settling suddenly on the far side of one of them, which makes it extremely difficult to follow. It is in its resting habits that it differs most from the mimetic group to which it belongs, for I have never seen a specimen settle anywhere except on a tree-trunk, and then always with its head downwards, just like a *Libythea* or the brown species of *Crenis*. The *Danainæ* and *Acræinæ*, on the other hand, always rest with their wings hanging down, and usually in more exposed positions; indeed, I think it may be said that no species of these groups (in South Africa at least) ever settles upon tree-trunks. This habit is also a very unusual one among our *Lycenida*, one or two species of *Teriomima* being the only cases of its occurrence which I can recall. Despite the great resemblance of this *Mimacræa* on its under-side to *Acræa encedon*, yet its colouring when at rest is very far from conspicuous, and harmonizes a great deal better with its surroundings than might be supposed from an examination of the insect in the cabinet, especially as the fore-wings are so much depressed between the hind-wings as to quite conceal the sub-apical white patch. The species seems to be of

considerable rarity; I know of only fourteen or fifteen specimens, all of which, except two or three, were captured by myself."

C. The Origin and Meaning of the Three Chief Forms of Limnas chrysippus.

I have often discussed the question set forth in the title of this sub-section with my friend Colonel J. W. Yerbury, who has observed this insect carefully in many of its localities, and is deeply interested in it.* He believes that the appearance of the various forms is controlled by environmental influences—dryness or moisture—acting upon the pupa at some critical period of special sensitiveness. The facts recorded below do not seem to be consistent with this interpretation.

My friends Mr. and Mrs. S. L. Hinde, who have kindly collected many specimens throwing light on problems to which I have given much thought (see also pp. 446, 447), sent me two series of forms of *Limnas chrysippus*, which are of special value in relation to this discussion.

The first set (of 15) was captured, almost on the sea-level, in the uniform damp heat of Mombasa, on May 6, 1900, and consists of four of the type-form of *Limnas chrysippus* (1 ♂ and 3 ♀), and eleven of the form *klugii* (9 ♂ and 2 ♀). All were taken in less than an hour on a spot of ground a few yards in extent. They thus afford a fair criterion of the proportionate numbers of the two forms.

The second set (of 13) was taken, at a height of about 5400 ft., at Machakos Road, on the Uganda Railway, on May 22, 1900, and consists of four of the type-form (3 ♂ and 1 ♀), one *alcippoides* (♂), seven *klugii* (2 ♂ and 5 ♀), and one *dorippus* (♂). These also were taken on a spot of ground a few yards in extent, in less than an hour.

Mr. Hinde has given me information as to the climate of the period in which the latter capture was made. It is printed on pp. 447, 448, but it is well to re-state here that May 22, 1900, was at "the end of a very dry wet-season in an exceptionally dry year." The specimens show the effect of these conditions, for they are on the average

* J. W. Yerbury, Journ. Bomb. Soc. Nat. Hist., 1892, p. 207. Col. Yerbury's observations on the species are also quoted by Dr. A. G. Butler in Proc. Zool. Soc. Lond., 1884, p. 478; 1885, p. 756.

very much smaller than those bred from larvæ which fed on the more luxuriant food-plant in Mombasa. Examining the two series, we are driven to the conclusion that the Machakos larvæ were partially starved, probably by feeding on parched food-plant. Interesting and important inferences may be drawn from the comparison.

In the first place the specimens, so far from supporting the conclusion often arrived at from incomplete and, as I think, ill-regulated experiments, that males are produced by starvation, actually show a larger number of females in a smaller total of specimens than the set from Mombasa, viz. 6 out of 13, as against 5 out of 15. Even if the females had been very scarce at Machakos, nothing would have been proved in the direction of the determination of the sex of the individual by diet, for starvation pushed to the extreme of preventing the completion of development of many individuals is certain to kill off the heavier sex far more freely than the lighter. The results, however, show no abnormal excess of males, and in every way support a prediction firmly founded on the anatomical fact that the essential organs of sex, the testis and ovary, are already present, rudimentary, but perfectly distinct, in the larval stage.

A comparison of the two series furthermore indicates very strongly that the various forms of the species are not in any way due to environmental causes, but are inherent and hereditary. It is believed that *klugii* is due to drought, but there is a larger proportion of this form in the series bred in the moist heat of the coast than in that reared at high and dry Machakos. The great difference in conditions which is manifest in the different average size of the two series was powerless to effect any change in the inherent hereditary tendency of the individual to become either *klugii* or its modification *dorippus*, the type-form or its modification *alcippoides*.

This comparison of forms from adjacent localities under different climatic conditions leads to an inference which is precisely the same as that drawn from the comparison of forms from different localities under the same climatic conditions. The tropical forests of West Africa and the Malayan Islands are very similar as regards climate: in the first *chrysippus* occurs as the white-hind-winged *alcippus*, in the second as the type-form, a peculiar dark form inhabiting Java (*I. bataviana*). It is not necessary

to pursue such comparisons further. So far as *chrysippus* is concerned, I know of no facts which support the hypothesis of the environmental production of the forms, and many which are inconsistent with it.

The only alternative hypothesis which presents itself is that of the operation of natural selection in determining the very different distribution of the various forms of *chrysippus* in the different parts of its range. And in attempting to solve this difficult problem I have been guided by the same principles which enabled me to suggest a meaning for the two widely-different seasonal phases of *Precis*, viz. the relation between insects and their enemies, the value of warning colours under certain conditions, their weakness and danger under other conditions. I believe that the condition of desert areas corresponds to that of the dry season, only differing in that they are more rigid, so that cryptic colouring is still more imperative. I therefore suggest that the *klugii* form is a development in a procryptic direction in areas where the struggle is so severe that even this most unpalatable and widely-mimicked species must put off some of its aposematic appearance, viz. the conspicuous black-and-white apex of the fore-wing.

There is also a peculiar faintly greenish-orange shade in the area of the apex of the fore-wing under-side beyond the sub-apical white bar of *chrysippus* which is wanting from the corresponding part of *klugii*, the difference tending to bring about a further uniformity in the ground-colour of the under-side of the latter.

Furthermore, many specimens of *klugii* have a ground-colour quite different from that of even light individuals of the type-form, gaining a distinct sand colour. This is all the more striking in Africa, where the type-form commonly develops a dark rich fulvous ground-colour very different from the paler Oriental type.

This interpretation is based on the assumption that *klugii* has developed from *chrysippus* and not *chrysippus* from *klugii*, and no escape from this assumption seems possible. The main lines of argument are these. Island individuals, which are so generally ancestral, are *chrysippus* and only very rarely *klugii*, except near the metropolis of the latter form in Somaliland. Perfect and imperfect mimics, Batesian and Müllerian, are very large in number, especially in Africa. Probably not one of them mimics

klugii and not *chrysippus*, a few mimic both, while the great majority mimic *chrysippus* alone. Again, *klugii* stands alone among *Danaina*, while the pattern of *chrysippus* is closely related to that of several other species and genera, such as *Salatura*. The distribution of *klugii* can be understood by supposing the desert region of Somaliland to be its centre. From this point it radiates, towards the east becoming gradually rarer, although it is well known in Karachi, and Colonel Yerbury even captured a single specimen in Ceylon, towards the south finally disappearing in South Africa, towards the Nile Valley, here also probably disappearing towards Central Africa. *Chrysippus*, or at least forms with a black-and-white apex to fore-wings, on the other hand, occur over the whole vast range of the species with the exception of certain parts of Somaliland.* The strongest argument is, however, one which is developed at the end of the section, because wide conclusions of great interest spring from it (see pp. 482-484).

The white-hind-winged *alcippus* was for a long time a great difficulty to me, but Mr. Marshall's suggestion (see p. 479) that it is a further development in the direction of still more efficient warning colours than the type-form seems to me to be sound, especially considering its distribution in the abundant life of the tropical West Coast, and considering the fact, of which Mr. Marshall assures me, that it is much more conspicuous on the wing.

I have for a long time thought that this great development of white, combined with the darkening of the fulvous ground-colour so common in African specimens and marked in *alcippus*, may indicate an incipient synaposematic approach to the black-and-white *Danaina* of the genus *Amauris*, and the large black-and-white *Acrainæ* of the genus *Planema*.

It is in favour of this view that the darkened ground-colour appears to be a recent development, although it has arisen in the Ethiopian region—the ancestral home of the species, if we may judge by the much larger number of mimics which resemble it in this part of its range. I believe the lighter ground-colour of *chrysippus* in India and, with certain exceptions, the East generally, formerly

* Consult Dr. A. G. Butler's map of the distribution of the forms of *chrysippus*, on Plate XLVI, accompanying his paper in Proc. Zool. Soc. Lond., 1884, p. 478; also by the same author, Proc. Zool. Soc. Lond., 1885, p. 756.

prevailed in Africa, because so many of its African mimics retain this shade rather than that now borne by their model, and because *chrysippus* itself often exhibits the paler tint, especially to the north and east* of the African continent (see pp. 471, 472.).

I quote below extracts from several of Mr. Marshall's letters dealing with the hypothesis which I have here set forth, and also referring in other ways to this interesting butterfly and its forms.

"*Malvern, May 14, 1897.*—I was interested to hear that the *L. chrysippus*, var. *alcippoides*, I sent resembles the West Coast specimens. Personally I have never come across that variety commonly, and those I have taken have mostly been very slightly marked with white, but Mr. G. H. Burn, who has collected for some years in the Tugela Valley, near Weenen, says they are not uncommon there, but apparently are most prevalent in the early winter (it is a very hot dry district), and they are frequently marked quite as strongly as the one I sent you."

"*Salisbury, Jan. 24, 1900.*—Referring to your very interesting remarks on *L. chrysippus*, I was much struck by your theory with regard to *klugii*. The only point, however, on which I do not feel satisfied is whether we can consider the colouring of this variety to be really protective. Of course I have never seen it in life, but I have seen many of the *inaria* form of *Hypolimnas*, and I must confess that the insect is very far from being inconspicuous; and even apart from colour it must be remembered that slowness of flight is a very important factor in rendering an insect conspicuous (compare our large and powerfully-armed but soberly-coloured wasps of the genus *Belcogaster*). Again, it would seem hardly consistent to regard the colouring of *klugii* as protective if we rank that of the smaller *Acræas*, which inhabit some at least of the same areas, as among the warning colours. It would therefore strengthen the theory if some other use could be assigned to the *klugii* coloration, though none occurs to me at the moment. Of course the correlation argument might be brought forward; but while thoroughly appreciating Meldola's masterly defence of this principle, I must admit that I have a distinct distrust in its use in such cases, as it means virtually begging the question. I cannot altogether gather from your remarks what are your reasons

* See F. A. Dixey in Proc. Zool. Soc., 1898, p. 373, note.

for supposing that the lighter Asiatic form is the older [see pp. 471, 476]. On general principles it would seem that swamping would be likely to keep the species more or less constant in its ancestral home, whereas those specimens that wandered further afield would probably tend to vary along slightly different lines; but perhaps I have not properly caught your idea. The case of *alcippus* would be a great deal more difficult to explain satisfactorily, seeing that it occurs also at Aden; and Butler says that examples sent from such places as Monbuttu, Wade-lai, etc., by Emin Pasha, showed every gradation from *chrysippus* through *alcippoides* to *alcippus*; further, if I remember rightly, you wrote me that an example I sent you from the Tugela had the white developed as strongly as in any West Coast specimen, and Burn said they were by no means uncommon there."

["A. G. Butler records (Proc. Zool. Soc., 1896, p. 243) Captain Nurse's statement that in Somaliland he bred all four forms of *chrysippus* from quite similar larvæ." G. A. K. M., 1902.]

"Salisbury, June 26, 1900.—Referring to the question of *Linnaus klugii*, although I fully appreciate the value of your arguments, yet I must confess that when looking at the matter from the point of view of an opponent of mimicry, it seems at least open to criticism. The difficulty seems to lie in the fact that the same coloration would thus have to be regarded as both protective and warning. Now you have said that in desert regions insects would be more liable to attack owing to the paucity of insect life, and I should be glad to know whether you have any special reasons for adopting this view, as I have no experience of what the conditions of life really are in such localities. But don't you think that it is more likely that the struggle for existence would be principally against climatic conditions and not so much a competition with other organisms, and that thus probably insects would have a better *proportionate* chance of finding a living than would the vertebrates as compared with more fertile regions? If this were so it would follow that insects would be comparatively freer from attack in desert regions, and this would afford us another explanation of the *klugii* phenomenon. We might presume that the less conspicuous *klugii* colouring was the more ancestral (as seems not unlikely), but that in the more fertile regions where

insectivorous vertebrates and invertebrates are so much more plentiful, this coloration was not sufficiently striking to guard it from the tasting experiments of these enemies, and thus the white bar would be gradually developed. The typical form would therefore supplant *klugii* in all places where there was greater need of more efficient warning colouring, and the latter form would only survive in those tracts where only a limited number of insectivorous enemies could exist. Such an explanation would further throw some light on the additional development of white in the hind-wing of *alcippus* in the prolific West Coast belt, where the increased number of vertebrate enemies requiring to learn by experience renders an additional conspicuousness advantageous. It seems to me that if such an explanation could be maintained it would be more consistent with our general views; but of course the matter hinges on the conditions of life in desert tracts, which is merely an assumption on my part."

"*Salisbury, Sept. 21, 1900.*—I was much interested in your remarks on the subject of *klugii*, and I quite agree that now that you have shown that my premise as to the conditions of life in desert countries is erroneous my contention falls to the ground. I should like to know how the range of the *inaria* form of *misippus* falls in with your proposition, and also whether you find the variety of *Acrwa encedon* without the white bar to follow the same range as *klugii*. I have found this variety [*dairu*] extremely rare in S. Africa, but a correspondent wrote me from Beira the other day that it was not uncommon there and promised to send me specimens."

"*Estcourt, Natal; Oct. 15, 1896.*—I had thought *Acrwa encedon* might be mimetic, but it must be a case of convergence—the type towards *Limnas chrysippus* and the variety *lycia* towards *escbria*. That this latter is the case I am led to believe by the fact that in Mashonaland only the type-form occurs and there *escbria* is also absent, whereas along the South-east Coast where the latter is plentiful, *lycia* occurs, and when I met with it in Durban I was struck with its resemblance on the wing to the whiter specimens of *escbria*, though this is not so apparent in the cabinet."

"*Malvern, Natal; Feb. 21, 1897.*—The case of *H. misippus* is however more puzzling than the *Euralias* which mimic *Amauris*. The *inaria* form of the female is

often cited as a mimic of *L. chrysippus*, var. *klugii*. Now this is by far the commoner form of the female *misippus* in S. Africa, whereas *klugii* appears to be extremely rare, in fact the single specimen recorded by Trimen is the only one I know of. How then can it be said to be mimicked by *inaria*? Again, *misippus* is recorded in several places in South America, where I believe *chrysippus* does not occur. It seems to require further investigation."

"*Umkomaas Mouth, Natal; Sept. 3, 1897.*—I certainly think that I have more frequently seen *Hypolimnas misippus* (female) in company with *L. chrysippus* than with its own male. The latter is fond of haunting the tops of kopjes in company with various species of *Precis* (which always occur in such localities), but I have never seen the female do so, neither does *chrysippus*."

The range of the forms of *eneceon* corresponds remarkably well with the forms of *chrysippus*. Mr. Marshall states above that the *klugii*-like form *daira* is extremely rare in the south where *klugii* is absent. Passing northward on the east side of the continent it gradually increases in proportionate numbers till it preponderates over *eneceon* where *klugii* preponderates over *chrysippus*. On the West Coast all forms seem to occur, but recently the white-hind-winged *alcippina* (Plate XV, fig. 7) has been found there in greater numbers than elsewhere. (Aurivillius, *Rhopalocera Ethiopica*, Stockholm, 1898, pp. 533, 534; Poulton, Proc. Linn. Soc. Lond., 113th Session, p. 6, Report of Meeting Dec. 20, 1900, where however the name *eneceon* is erroneously printed *unicolor*.) The distribution of the Lycaenid mimic corresponds equally well, *marshalli* with *chrysippus* in the south (Mashonaland), *dohertyi* with the predominant *klugii* in British East Africa. *H. misippus* ♀ shows upon the whole an almost complete lack of correspondence, for *inaria* is common nearly everywhere, while *klugii* is confined to the range described on p. 476. In British East Africa, however, *misippus* ♀ corresponds well with the two forms of its model; while on the west, where *alrippus* is the only form, the want of geographical coincidence is most striking, for the *inaria* form is relatively abundant, while neither in it nor in the type-form, so far as I am aware, is there any special tendency towards the development of white in the hind-wings. It is a striking fact that the Acreine mimic should exhibit so close a coincidence with the geographical range of its Danaine

model, while the Nymphaline mimic shows such a marked want of correspondence. The comparison may help naturalists to realize the great importance of Müllerian mimicry and the searching selective process which has brought it about.

I have for many years attributed this want of correspondence between the commonest mimic of *chrysippus* and its model, to the wide-ranging powers of the former butterfly and its great tendency to wander, combined with some special protection which there is reason to believe it possesses, rendering its resemblance synaposematic rather than pseudoposematic. There are in the Hope Department three females (two of them *inaria*) and two males of *H. misippus* captured out of a swarm through which the ship *Winefred* passed in May 1893, when she was on the Atlantic over 500 miles from land (Ent. Record., vol. xii, No. 11, p. 315). The Müllerian resemblance of *misippus* ♀ to *chrysippus* was suggested by the present writer at the meeting of the American Association for the Advancement of Science in 1897 (see vol. xlvi, p. 242, where arguments in support of this conclusion may be found). Extracts on this subject from Mr. Marshall's letters are printed below:—

“*Malvern, Natal; Oct. 7, 1897.*—I fear I cannot at present accept your suggestion that *Hypolimnas misippus* is itself protected. I may be wrong, but in these matters I depend more than anything on the habits and actions of the insects as I have seen them when undisturbed and when frightened. There is to my mind a radical difference between mimics and their models (as opposed to convergent forms) which is often very difficult to define. There is also a structural difference which appeals to me, so that I believe I could almost tell one from the other with my eyes shut merely by the feel of it in the net. To give an instance: when on a short holiday trip to the rich Mazoe Valley in December 1894, I started out on Christmas Day with the set purpose of catching something “good” to commemorate the occasion. While strolling along the narrow belt of thick bush which there fringes the river, I saw flying leisurely in front of me what I took to be a very small and brightly-coloured specimen of *Limnas chrysippus*. I coveted it, and a few seconds later it was in my net, through the folds of which I could but indistinctly see it, so that I was still deceived. But no sooner

had my finger and thumb met across its thorax than my heart beat high with that keen excitement that every ardent entomologist feels when he has found some unexpected treasure—for I knew I had got a new mimic of *chrysippus*! A short inspection showed it to be a new Lycænid—a *Mimacrava* (since named *M. marshalli*, Trimen). On the other hand, when I caught my first specimen of *Aletis* here in Malvern in March 1893, I remember it puzzled me much, for I felt sure it was not a mimic of *chrysippus*, and yet I could not understand the reason of the colouring, for I was then unaware of Müller's theory.

"To return to *misippus*, although I admit it is a somewhat difficult case, yet the fact that it has elected to mimic what I take to be the hardest and best-protected butterfly in Africa, combined with the general adaptability to varying conditions which one would expect it to share with its nearest allies the Junonias, must I fancy go a long way towards explaining its wide range and comparatively large numbers. There is another factor that must not be overlooked, and that is that through a considerable portion of its range in South-east Africa at all events it is the only butterfly which shows mimicry of *chrysippus*. This is particularly noticeable on the rolling grass veldt of the inland plateaux where *chrysippus* is particularly abundant.

"I think your idea as to the latter insect having originated in Africa is excellent and in every way most probable."

"*Salisbury, March 6-10, 1898.*—The facts that you mention with regard to *Hypolimnas* are certainly very curious, and would seem to be only explicable by presuming the species you mention to be protected. But in the case of *Hypolimnas misippus*, after reviewing the general habits and attitude of the female, I cannot bring myself to believe that it is anything but a true Batesian mimic. Might it not be a similar case to that of the genus *Papilio*, in which we have the distinctly protected and distasteful *P. coon* and at the same time the clearly mimetic *P. cenea*?"

D. *A Study of Mimetic Forms may enable us to reconstruct the Lost Stages through which the Older Model has passed.*

If *klugii* has been derived from *chrysippus* we should expect to find traces of the markings of the latter upon the wings of the former. And as a matter of fact faint

indications of the white sub-apical bar of *chrysippus* can be detected in *klugii*, especially at the points on the costa and the hind margin which the two ends of the bar would have reached. Very faint traces of the course of the bar between these two points can be made out in certain individuals (Plate XV, fig. 1), while occasionally they are very distinct, especially upon the under-side (Plate XV, fig. 1a). Looking at these two figures, and comparing them with Figs. 1 and 1a on Plate XIV, it is impossible to resist the conclusion that we see before us the vestiges of a fading character and not the rudiments of a developing one. It is interesting to note that one of the slightly intermediate varieties of *klugii* here represented (viz. Fig. 1, Plate XV) was an individual captured by Mr. and Mrs. Hinde at Machakos Road, and that three or four others of the same set showed similar tendencies. It may be that the unfavourable conditions (see pp. 473, 474), although unable to change one form into another, nevertheless administered a shock which caused a slight reversion towards the ancestral type in some individuals.

The three great mimics of both forms of *chrysippus*, the female of the Nymphaline, *Hypolimnas misippus* with its *inaria* form mimicking *klugii*; the Acraeine, *A. encedon** with its *klugii*-like form *daira*; the Lycænid *Mimacræa marshalli* with what I believe to be merely its *klugii*-like form *dohertyi*, all these show precisely the same thing as their model only in an exaggerated form, because the mimic follows its model and therefore still exhibits stages which the latter has left behind. Comparing the upper- and under-side of the *chrysippus*-like Lycænid on Plate XIV (Figs. 2 and 2a) with those of the *klugii*-like form on Plate XV (Figs. 2 and 2a), there can be no doubt that the latter developed from the former. The white bar of *marshalli* (Plate XIV) can still be distinctly traced in *dohertyi* (Plate XV), not indeed as a white bar but as a very faint paling of the ground-colour over a sub-apical area, the outline of which exactly

* The first recognition of the mimicry of *chrysippus* by *encedon*, and indeed of the existence of Müllerian mimicry in the Ethiopian Region, was first brought forward at the meeting of the British Association at Toronto in 1897 (Report, p. 689). Aurivillius (Rhop. Eth. 1898, p. 533) states that the resemblance had not been previously noticed. The account given by Aurivillius is however far more complete than that in the brief abstract here referred to, and is also accompanied by illustrations.

corresponds to the bar itself. The comparison to a pseudo-morph suggests itself; the bar is indeed absent but its shape is there. The case of the Acraeine mimic is still clearer, Figs. 3 and 3a on Plate XIV bearing the same relationship as that above described in *marshalli-dohertyi*, to Figs. 3 and 3a on Plate XV. The same "pseudo-morph" of the white bar can be seen in the latter, while in Figs. 4, 5, and 6, on Plate XV, some by no means uncommon intermediate varieties between *ecedon* and *daira* are represented. Fig. 7 shows the form *alcippina* which resembles *alcippus*, the white-hind-winged *chrysippus*.

When a geologist finds a recognizable fragment of one rock included in a stratum of another, he is usually safe in inferring that the latter is the younger. With equal confidence the zoologist may conclude that the mimicking species is younger than the species it mimics. The latter must have been in existence before the former attained a resemblance to it. From this point of view the comparison between *chrysippus-klugii* and their mimics is of intense interest. *Chrysippus* and *klugii* are now well defined the one from the other, and it is probably impossible or at least extremely difficult to get a series of intermediate forms between them. If we had not the mimics we might well believe that *klugii* arose ready-made from *chrysippus* by a process of discontinuous or transilient evolution. But two of the younger mimics are very common and widespread, and both *missippus-inaria* and *ecedon-daira* present us with abundant varieties showing every grade of transition from the one form to the other. Of the Lycænid less can be said. It is still extremely rare (see pp. 472, 473) and at present only known in two widely-separated areas. But even in it the gap *marshalli-dohertyi* has been shown above to be much less wide than that of *chrysippus-klugii*. We are led to believe from this comparison that in some earlier age the two forms of the Danaïne model existed in the stage now reached by their commonest mimics, and, like these, were connected by a series of abundant intermediate varieties which have since been obliterated by selection.

E. *Amauris echeria*-like Group: Marked Secondary Resemblances between the Forms mimicking *echeria*.

This species of *Amauris*, with its very characteristic rectangular buff patch on the hind-wing and buff or white-

spotted fore-wing, is the dominant Danaine of South Africa, and extends in considerable abundance right up the east and east central parts of the continent well into British East Africa. It is a centre of convergence for several *Nymphalinae* and *Papilioninae* in the same district.

An interesting group, captured by Mr. Marshall at Malvern, on March 25, 1897, consists of the following species:—

Amauris ccheria, var. *albimaculata* ♂.

2 *Euralia nima* ♀.

Papilio cenea ♀, *cenea*-form, with white spots on fore-wing, like the var. *albimaculata* of *A. ccheria*.

Papilio leonidus, var. *brasidas*.

The last-named *Papilio* is a somewhat outlying member of the group, being separated from the others by the patch on the hind-wing, which is white with a faint greenish tinge, instead of buff. The general arrangement of the light markings on the black ground is however similar, and Mr. Trimen states that "it was in the habit of settling precisely in the way affected by the *Amauris*, viz. on a projecting leaf or twig, with the wings closed and hanging downward, and in this exposed position remaining motionless for a considerable time" ("South African Butterflies," vol. iii, 1889, p. 216). In two points, viz. size, and contour of the wings, it is more like the Danaine model than any of the other above-mentioned species.

The most interesting point about the group as a whole is, however, the undoubted secondary resemblance between the species which primarily resemble the *Amauris*. The secondary resemblance is, moreover, even stronger between *P. cenea* and the *Euralia* than between either of these and *P. brasidas*, that is to say, the species exhibiting a closer primary mimicry also exhibit a closer secondary mimicry. This fact suggests that the secondary resemblance is of permanent value and not a mere phase which will ultimately be lost in the primary resemblance. Mr. Marshall informs me that these secondary mimetic resemblances are still more marked upon the wing, so that a naturalist may often be sure that he sees before him a mimic of *ccheria* or of a black-and-white *Amauris*, but cannot in any way distinguish the mimic itself as *Papilio*, *Pseudacraea*, *Hypolimnas*, etc.

The points in which the mimics of *A. ccheria* converge together and diverge from their primary model are as follows:—

- (1) Size: They are much larger than their primary model. *Brasidas* is in this respect intermediate.
- (2) Scalloped outline of hind-wing; feebly marked in *brasidas*. Slight indications of scalloping are intensified in *ccheria* by the fringe being marked by two white spots in each of the shallow concavities. This is only distinct in some individuals, apparently chiefly from the northern part of the range. The marked concavities of the mimics are also intensified by whiteness.
- (3) Elongated oval shape of largest spot in fore-wing, viz. the spot below the cell, while that of the model is nearly circular. The long axis of the oval spot furthermore assumes the same direction in each of the three species, while that of *ccheria* is entirely different.
- (4) The *much* greater prominence in all three mimics of the sub-marginal row of white spots on the upper-side of both wings.
- (5) Strongly-marked black internervular rays pass inwards from the margin of the hind-wing of *Euralia* and invade the periphery of the ochreous patch, uniting with the black veins to make up a pattern of radiating dark lines. The radiate appearance of the under-side is even more prominent than that of the upper-side. *Papilio cenea* ♀ is very similar, except that the upper surface exhibits only faint indications of the character (which however is strongly marked in the *hippocoon* form resembling *Amauris dominicanus*).*

Some of these differences between mimics as a whole

* In this respect, viz. the prominent development of internervular rays on both surfaces of the hind-wing, the *hippocoon* form of the Western *P. merope* presents a far closer resemblance to its co-mimic *Euralia anthedon* than to the primary model *Amauris niarius*, and similarly the *hippocoon* form of the Southern and Eastern *cenea* to *Euralia wahlbergi* than to *Amauris dominicanus*. Not only is there the conspicuous radiate appearance wanting in the Danaine model, but the white centre of the upper surface of the wings deepens gradually at its margin into black in both *Papilio* and *Nymphalid*, while the margin of the corresponding white area in the Danaine exhibits an extremely sharp and abrupt transition into black.

and their primary model are less pronounced in the northern part of the range, in British East Africa, where the *Amauris* is often larger and commonly possesses far more distinct sub-marginal spots on the upper-side. It is interesting to compare other mimics of *echeria* with the members of the group captured by Mr. Marshall at Malvern on March 25, 1897.

The female of *Pseudacraea tarquinia* is a poorer mimic of *echeria* than *Euralia mima* and *Papilio cenca* ♀, although upon the wing the resemblance is doubtless strong. In size it closely approaches the model: it has a slightly-scalloped border, and an irregular oval spot with a direction similar to that of the other mimics; the marginal spots are small as in the southern *echeria*. On the under-side of the hind-wing is a basal brown patch with conspicuous round black spots as in many Planemas. In the development of internervular black stripes invading the squarish ochreous patch on the hind-wing it resembles *Euralia* and diverges from the Danaïne model.

The female of *Papilio jacksoni*, in the shape and direction of the spot below the cell on the upper-side of the fore-wing, far more closely resembles *echeria* than any other mimic I have seen. On the other hand, the hind-wing is deeply scalloped, the effect being much intensified by white-margined concavities, the sub-marginal spots are as a whole larger than those of any other mimic, while the under-surface of the hind-wing exhibits very little approach towards the *Amauris*, retaining the basal, black-spotted brown triangle of the male, that well-known synaposeme and pseudaposeme of many Ethiopian Papilios, Planemas, Acraeas, Elymnias, Pseudacraeas, etc., unknown in the Ethiopian *Danainæ*. Thus, in addition to its primary mimicry of *echeria*, var. *albimaculata*, *jacksoni* manifests secondary mimetic resemblance to the former group of Rhopalocera, especially the Planemas, and also an approach to other mimics of *echeria* in its conspicuous sub-marginal spots and deeply-scalloped border. The general effect of the spotting of the fore-wing is also more like that of *P. cenca*, and even of *Euralia mima*, than its primary model.

The female of the south-eastern *Papilio echerioides* is very similar to that of *jacksoni*, but the spot below the cell of the fore-wing is oval and in shape and direction more nearly resembles that of *Papilio cenca*.

F. *The Origin of the black-marked, golden-brown Triangle at the base of the Hind-Wing under-side in many Ethiopian Butterflies.*

Mr. Roland Trimen, F.R.S., considers that the black-marked, triangular, golden-brown basal patch on the under-side of the hind-wing of the female *P. cynorta* which mimics *Planema gea*, and *P. echerioides* [and we may now add *P. jacksoni*] "points to the inference that mimicry of the *Planema* group was in both these *Papiliones* the earlier tendency, and has only more recently been diverted in the direction of *Amouris* in the case of the Southern species"; for "this character is in the ♂s of *cynorta* and *echerioides* even more developed than in the ♀s, and is in direct mimicry of the *Planema*" ("South African Butterflies," vol. iii, 1889, p. 258). But if in the female of *cynorta*, which is admitted to be an excellent *Planema* mimic, this very character is reduced, how can it be believed that its greater development in the male is a case of direct *Planema* mimicry, seeing that in every other respect this sex, if a mimic at all, is a most imperfect one?

A comparison of the *Papilios* and *Planemas* with the most remarkable development of this warning character at the base of the under-side of the hind-wing renders it probable that in this respect the latter have acted as Müllerian mimics rather than models. The character is far more highly developed and specialized in a section of Ethiopian *Papilios* than in any of the *Planemas*: it also appears in forms which are unknown, and accompanied by other warning characters which are also unknown in the *Planemas*; it reaches its highest development in species which do not mimic *Planemas*. It is also probable that the conspicuous, sharply-outlined white band of the male *echerioides*, *cynorta*, etc., nearly alike on both upper- and under-sides, is a warning character peculiar to this group of tailless Ethiopian *Papilios*. In the most strongly-marked species, with sexes nearly alike (*zenobia*, *cypræofila*, etc.), the outer margin of the band on the fore-wing is coarsely serrated in a very characteristic manner on both surfaces. Furthermore (in *cypræofila*, *gallicenus*, etc.), another warning character of great interest is added in the row of large conspicuous marginal white spots on both surfaces of the hind-wing and smaller ones on the fore-wing. In this respect this group of *Papilios* presents an exact

negative of the positive form of synposeme characteristic of the Pierine genus *Mylothris*. Thus very striking warning characters are peculiar to this section of Papilios, the fifth or Zenobia Group of Aurivillius; and, furthermore, the character we are specially considering, the black-marked basal patch of the under-side of the hind-wing, assumes a form which is unknown in *Planema*, being traversed by blackened veins and broader black internervular lines. In the species of *Papilio* last mentioned there are no spots upon the brown triangle, only these strongly-marked radiating lines. In *zenobia* and still more in the male *cyorta* a few spots are added by modification of some of the other markings, and it is probable that this slight change is a late diaposematic response to *Planema*, made after the latter had gained the golden-brown triangle in Müllerian mimicry of these dominant Papilios.

Another important point is the fact that the golden-brown triangle is *larger* in the females than the males of *cypræofila* and *zenobia* which do not mimic Planemas, *smaller*, as has already been pointed out, in the females of the species which strongly exhibit this Müllerian approach to either *Planema* or *Amauris*.

It must also be remembered that Papilios may be excessively unpalatable to insect-eating animals as a whole. Thus Mr. Frank Finn concludes that *P. aristolochiæ* is more distasteful to birds than *Danainæ*, *Acraea violæ*, and *Delias eucharis* (Journ. Asiat. Soc. Beng., lxxvii, pt. ii, 1897, p. 614).

The facts and arguments set forth above render it probable (1) that the golden-brown triangular patch first arose in the Zenobia Group of Ethiopian Papilios; (2) that it was later reproduced on a smaller scale by the Acraeine genus *Planema*, the Acraeine round black spots contrasting with the ground-colour in place of the radiating black lines of the *Papilio*; (3) that, later still, other widely-separated genera reproduced the character in the form it had assumed in *Planema*, e. g. *Pseudacraea*, *Elymnias*, etc., while a reciprocal (diaposematic) tendency (see p. 426) to approach the *Planema* form is seen in certain species of the Zenobia Group of Papilios. Several species of the group have females mimicking Acraeines or Danaines. In the three of these which were examined the males exhibited the above-described diaposematic tendency, while the females possessed a greatly-reduced but otherwise similar triangular patch.

Hence this characteristic widespread Ethiopian synaposeme and pseudaposeme has probably originated in a diaposematic fusion of the triangular golden-brown patch of the Zenobia Group of Papilios with the scattered circular black spots which are characteristic of Ethiopian Acraeas. I have made much use of Aurivillius' admirable "Rhopalocera Ethiopica" in this section which is devoted to the discussion of an under-side synaposeme, although the distinguished author himself maintains that mimetic resemblance is almost confined to the upper-side of butterflies' wings—a very strange conclusion (*loc. cit.*, p. 535).

G. *Compound Group containing Representatives of all the three previously described. Species probably entering two Groups.*

The groups described above fly together, and thus represent in a compound group the chief types of butterfly coloration which a young insect-eating animal of South and Eastern Africa requires to learn, by a trial of one or more representatives. The following members of the three groups were captured by Mr. D. Chaplin at Berca, a suburb of Durban, on April 5, 1896, and are now in the Hope Department.

BLACK-AND-WHITE GROUP.

Amauris ochlea.
Planema aganice ♀.

Echeria-LIKE GROUP.

Amauris echeria, var. *albimaculata*.
Euralia mima.

Chrysippus-LIKE GROUP.

Limnas chrysippus ♂.
2 *Hypolimnas misippus* ♂, ♀ type-form.
2 *Acraea petraea* ♂ ♀.
2 *Acraea encedon*, type-form and var. *Lycia*.

That the same species may produce two or more forms entering as many groups is well known, but, as a rule, such polymorphism is confined to the female sex. In the polymorphism of *Acraea encedon*, however (see pp. 483, 484), we have a case in which both sexes are present in the various forms, and although the relative numbers of the forms are very different and certain of them may perhaps be absent from a district, I know of no case in

which one alone is found in any part of the total range of the species. Hence the polymorphism, although partially a distributional phenomenon, is not entirely so. On the other hand, I know of no example among the Lepidoptera in which a species is at the same season divided into two sub-equal sections throughout its range, each containing both males and females, and each section mimicking a very different model. Among Diptera, the European *Volucella bombylans* and its form *mystacca* supply good examples; and now Mr. Marshall has collected evidence which makes it in the highest degree probable that the Lepidoptera are not without such cases. He brings convincing support for the belief that *Euralia wahlbergi* and *E. mima* are the two forms of a single species. It is greatly to be hoped that Mr. Marshall may be as successful in establishing this interesting and unique case, as he has been in the marvellous seasonal transformation of *Precis*. His evidence is set forth in the following quotations from his letters:—

“*Umkomaas Mouth, Natal; Sept. 3, 1897.*—In my own mind I am pretty well convinced that *Euralia mima* and *wahlbergi* are one and the same species which has developed two mimetic forms as in *Papilio cenea*, but that in this case both sexes are concerned. My reasons for so thinking are that they have been taken *in coitu* several times, that specimens occur presenting intermediate coloration, and also that the two forms are always found together whenever they are met with in any number. I have not often been fortunate enough to see these congregations, but I remember seeing some thirty or forty specimens, comprising about equal numbers of each form, collected together on the side of a steep shady kraantz along the Palmiet River. Mr. A. D. Miller, who has collected for many years in Durban, tells me this is by no means uncommon, and that they congregate particularly in the afternoon when going to roost. Mr. C. N. Barker tells me that some years ago he came across a large number of both forms on a large tree on which they had evidently bred, for many of them had only just emerged, and some had not their wings fully developed. This shows that they are also associated in their earlier stages.”

About the time when this passage was written Mr. Marshall presented to the Hope Department a set of eight individuals of these Euralias, viz. four of *E. mima* (2 ♂,

2 ♀), and four of *E. wahlbergi* (3 ♂, 1 ♀), which he had captured on the Umbilo River, near Durban, Natal, on June 28, 1897. His account of the habits of this little company is given below.

"*Malvern, Natal; Oct. 7, 1897.*—The specimens of *Euralia mima* and *wahlbergi* were captured going to roost together on a small clump of ferns under a steep kraantz between 3 and 4 p.m. Although disturbed a good many times in my efforts to catch them, they always returned after some minutes. There were two others which were too tattered to keep, and two more that I failed to catch."

If Mr. Marshall's conclusion be established, it follows that the corresponding and closely-allied mimetic West African forms *Euralia anthedon* and *E. dubia*, connected like *wahlbergi* and *mima* by intermediate varieties, are similarly the dimorphic forms of a single species.

H. Groups of Synaposematic *Acras* captured at the same Place and Time.

Professor Meldola first suggested the use of Fritz Müller's principle to explain "the prevalence of one type of marking and colouring throughout immense numbers of species in protected groups, such as the tawny species of *Danaïs*, the barred *Heliconius*, the blue-black *Euphas*, and the fulvous *Acras*" (Ann. and Mag. Nat. Hist., ser. 5, vol. x, 1882, p. 425). As an example of Müllerian mimicry in the last-named group, I was anxious to obtain convergent species captured in one place and at one time. Mr. Marshall very kindly obtained two such groups for me. The first was captured by him on Dec. 31, 1898, at Salisbury, and contains the following species:—

- 6 *Acrava doubledayi*, var. *acina*, 4 ♂ 2 ♀ (♂ Fig. 1, ♀ Fig. 2, Plate XVI).
- 4 *Acrava caldarena*, 3 ♂ 1 ♀ (♂ Fig. 3, ♀ Fig. 4, Plate XVI).
- 4 *Acrava nohura*, var. *halali*, 2 ♂ 2 ♀ (♂ Fig. 5, ♀ Fig. 6, Plate XVI).
- 2 *Acrava violarum*, var. *asema*, 2 ♀ (Fig. 9, Plate XVI).
- 2 *Acrava rahira*, 1 ♂ 1 ♀ (♂ Fig. 7, ♀ Fig. 8, Plate XVI).

All these species are of approximately the same size and shape of wing, colour, and pattern, *rahira* being furthest

removed from the average appearance of the group, while *caldarena* is an outlying member in one respect only, viz. the pronounced apical black patch on the fore-wing. The brightly-coloured males and the brightest of the females of all these species would closely resemble each other on the wing, including the male of *violarum*, which was not captured on that particular day; and similarly a uniform effect would be produced by the darker females. The under-sides of all species except *rahira* are superficially alike. The strong superficial resemblance is well shown in Figs. 1 to 9 on Plate XVI.

A second group was captured at Salisbury on Jan. 7, 1899, and contains the two following species:—

2 *Acræa anemosa* ♂ ♀ (♀ in Plate XVI, fig. 10).

2 „ *natalica* ♀ (Plate XVI, fig. 11).

These large *Acræas* are obviously very different in the details of coloration, but the positions in which the black marking of the upper surface are massed on the fulvous ground-colour are almost exactly the same, the only marked difference being the presence of numerous black spots in the first-named species which are almost absent in the second. Mr. Trimen speaks of *anemosa* as “in habit and general colouring very near *natalica*” (*loc. cit.*, vol. i, p. 156). The under-sides are far less alike, but there can be no doubt about synaposematic convergence having occurred. It is probable that the approach has been chiefly, perhaps entirely, on the side of *natalica*, which has adjusted markings of a type usual among Ethiopian *Acræinæ* in such a manner as to produce superficial similarity to *anemosa*, an *Acræa* in which a very remarkable and unusual appearance is the warning sign of exceptional defence against insect-eating animals (see p. 413).

Mr. Marshall informs me that the two species are very similar upon the wing, and that the resemblance is much closer in the case of the female *natalica* than the male, thus following the rule in mimicry, and confirming still further the opinion expressed above that the approach has been from the side of *natalica*.

I. *Mimetic Species of South African Lycænidae and Hesperidae captured with their Models.*

Exclusive of *Mimacræa marshalli* and its form *dohertyi*

which were discussed in relation to their models *chrysippus* and *klugii*, the groups containing *Lycanidæ* or *Hesperidæ* are considered below.

A group of the smaller *Acræas* with a single mimetic *Lycanid* was captured at Salisbury on Sept. 28, 1900. It contains the following species:—

- 2 *Acræa violarum*, var. *usema* ♂.
- 1 „ *doubledayi*, var. *axina* ♂.
- 1 „ *induna* ♂.
- 1 *Catochrysops mashuna* ♂ (figure of ♀ on Plate XIV, fig. 5).

A. induna falls into the first-mentioned group of small *Acræas*, resembling *caldarena* in the possession of a black apical patch to the fore-wing. The strong development of black spots upon an ochreous ground on the under-side of the *Lycanid* is doubtless mimetic in the position of rest, especially when in the company of *Acræas* or in places where they are likely to be found. Mr. Marshall informed Mr. Trimen “that on October 20, 1894, he saw two of this *Lycæna* sleeping on the end of a stem of dry grass among a number of *Acræa nohara* and *A. caldarena*, and was struck with the general similarity of their under-side to that of the *Acræas*; he also noticed that in the attitude of repose the fore-wings of the *Lycæna* were well depressed between the hind-wings, giving the insect the elongate outline of an *Acræa*” (Trans. Ent. Soc. Lond., 1898, p. 6). Mr. Trimen also suggests that the heavy black spotting of *L. (C) gigantea* and *L. (C) perpulchra* (Trim.) [= *peculiaris*, Rog.] is of the same significance, although the ground-colour is not *Acræa*-like in these species.

A paragraph from one of Mr. Marshall's letters is quoted below.

“*Umkomwas Mouth, Natal; Sept. 3, 1897.*—The under-side of the *Acræa*-like *Lycanid* *L. mashuna* is ochreous yellow with large black spots, but I did not realize its resemblance to an *Acræa* until I saw them roosting together. The mimicry, however, is in a very incipient stage, for the yellow under-side fades somewhat rapidly, thus much lessening the resemblance; and, as it does not occur in its near allies *L. hypoleuca* and the fine *L. gigantea*, it is clearly a recently-acquired character.”

In another group captured at Umtali, 3700 feet, in December 1900, the *Acræas* are only represented by a single

species, and that not specially suitable as a model for the other members. The great interest of the assemblage is the presence of a rare Hesperid, *A. tettensis*, in which black spots and a pale pinkish tinge on the under-side of the hind-wings appear to indicate strongly-marked mimicry of *Acræas* on a line along which the above-named *Lycænids* have advanced to a greater distance. In another respect, however, viz. the strongly-marked black-and-white margin of the hind-wing under-side, the Hesperid is a much closer mimic of a general *Acræa* type. Mr. Trimen also speaks of the spotting and tinting of the under-side of both wings of this species as very peculiar and strongly recalling the aspect of some of the smaller *Acræas* (*loc. cit.*, vol. iii, p. 338).

I have received from Mr. Marshall the following references to the two Hesperids in the list of species making up this group:—

“*Salisbury, Jan. 11, 1901.*—I have recently obtained at Umtali another Hesperid, the very rare *Abantis tettensis*, showing strong *Acræoid* coloration on the under-side, which I will send you together with a *Kedestes*, which is of interest as it shows the incipient stages of such mimicry.”

“*Salisbury, Sept. 27, 1901.*—I have never seen *Abantis tettensis* with its wings closed over its back; all that I have captured rested with wings expanded horizontally. Indeed I cannot at the moment recollect ever seeing any *Abantis* settle with vertical wings. I think it is highly probable that *tettensis* would sleep in that position, but under the circumstances I should not like to assume it as a fact without actually seeing it.”

The group is as follows:—

- 3 *Acræa concedon*, type-form.
- 2 *Catochrysops peculiaris* (Plate XIV, fig. 4).
- 2 *Abantis tettensis* („ „ „ 6).
- 1 *Kedestes macomo*, var. („ „ „ 7).

In the latter Hesperid the brilliant ochreous under-side affords an effective background for the small but distinct black spots on the under surface of both wings. The general effect is somewhat *Acræa*-like, but the tint of the under-side of most smaller *Acræas* is pinkish when they are fresh.

A more perfect Hesperid mimic is seen in the rare *Baoris netopha*, of which a female (Fig. 13, Plate XVI) was

captured by Mr. Marshall at Salisbury on April 6, 1898, together with a male of *Acræa doubledayi*, var. *avina* (Fig. 12, Plate XVI), which is one of the many smaller *Acræas*, to which it bears a somewhat generalized resemblance on the under-side of its wings in the natural position of rest, which is nearly but not quite represented in Fig. 13 (see the description of the Plate). Mr. Marshall has sent the following account of the attitude:—

“*Salisbury, Feb. 12, 1899.*—The *Baoris netopha* rest with closed wings, and the fore-wings pressed well within the hind-wings so as to hide the white spots; they then look much more *Acræa*-like.”

The curious reticulate under surface of the hind wings of the isolated and remarkable Hesperid *Cyclopides willemi* is mimetic of the probably distasteful *Alæna nyassæ*, which possesses a somewhat similar but much coarser reticulation. Mr. Marshall states that the resemblance is much enhanced in the resting attitude of both species by the concealment of the fore-wings, with the exception of the apex, within the hind. Both species frequent the same localities, and both rest upon grass-stems. One of each species was captured at Salisbury on Feb. 23, 1901, and another similar pair on March 3, 1901.

In thus bringing together Mr. Marshall's examples of mimicry in *Hesperidæ*, it is appropriate to include the following interesting case of mimicry on the part of a Hesperid for a Danaine larva.

“*Salisbury, March 10, 1898.*—The larva of the large ‘skipper’ *Rhopalocumpta forestan* possesses a colouring wonderfully similar to that of *L. chrysippus*, though it lacks the filaments. I only know the larvæ of three other species of *Hesperidæ* and they are all green; moreover, they form shelters for themselves, and never come out to feed except after dusk; whereas, although *forestan* also forms a shelter, yet it frequently comes out and feeds in broad daylight, when it is a very conspicuous object.”

The upper-side of *Alæna nyassæ* appears to fit in with the strong combination of black-and-white Ethiopian butterflies belonging to the *Danainæ* and *Acræinæ* and their Batesian and Müllerian mimics. Among the smaller of the latter *Neptis agatha* is probably to be placed, and this species is on the wing with the much smaller Lycænid. Thus Mr. Marshall has sent to the Hope Department specimens of the *Neptis* captured at Salisbury on March

19 and May 1, 1898, and of the *Alæna* taken on March 20 and April 3 of the same year.

It occurred to me that *Castalius calice* might also belong to the same group, but Mr. Marshall points out, in the passage quoted below, that its habits do not support this view.

"Salisbury, Jan. 8, 1899.—I should very much doubt whether *Castalius calice* is convergent with or even a mimic of *Alæna nyassæ*. Their habits and stations are very different, and moreover *C. calice* (of which I believe *C. melæna* will prove to be the summer form) is common in Natal and the Transvaal, where *A. nyassæ* does not occur. I should not regard *C. calice* as an unpalatable species, and its colouring is by no means conspicuous owing to its small size: it is an active little insect resembling *T. plinius*, *Lycænesthes*, and other arboreal *Lycænidæ* in its habits. In the intense light and shade of this climate its black-and-white markings are rather protective as it rests on the shiny leaves of its food-plant (*Zizyphus*), just as are the brilliant white under-sides of some *Iolai*. The convergence you suggest between *A. nyassæ* and *Neptis agatha* and *Nyctemera leuconoë* is highly probable, but *Amauris* and the black-and-white *Acræas* are all absent from the Mashona plateau, being all coast or low-veldt forms. *Alæna*, *Pentila*, and perhaps *Deloneura*, are in my opinion the only unpalatable South African *Lycænidæ*, and the latter is more likely to be a mimic of some day-flying moth. *Catochrysops mashuna* used to be very abundant here, but only occurring in September and October. I only saw two or three this season and always when I had no net."

Three specimens of another interesting and probably distasteful species of the same *Lycænid* genus *Alæna amazonula* captured on the same day, Sept. 26, 1897, as the conspicuous day-flying and probably unpalatable geometrid moth *Pctovia dichroaria* were presented by Mr. Marshall to the Hope Department. Mr. Marshall had taken the group in the same locality at Malvern, Natal, and, as the passage from his letter quoted on p. 498 indicates, he believes that the resemblance is synaposematic. In the cabinet the likeness is stronger on the under than upon the upper surface, but is probably strongest of all upon the wing.

Alæna amazonula is a *Lycænid* of great interest, probably exhibiting a generalized Müllerian resemblance to the

Acræas. Although unlike any single species of *Acræa*, the likeness to this group and unlikeness to the *Lycænidæ* was sufficient to deceive Boisduval and at first Roland Trimen (Rhop. Afr. Austr., 1862-66, p. 111). In the Hope Collection also I found it had been placed among the Acræas by Professor Westwood. Its undoubted Lycænid affinities were finally established by Roland Trimen ("South African Butterflies," vol. ii, 1887, p. 222).

The above-mentioned errors as to the affinity of this aberrant Lycænid certainly support the opinion that it bears a general resemblance to the *Acræinæ*. It would be interesting to know its resting habits. With the underside exposed and the long narrow wings it would probably bear some general likeness to a very small *Acræa*. Mr. Marshall wrote concerning it as follows:—

"*Umkomaas Mouth, Natal; Sept. 3, 1897.*—*Alena amazoula* is certainly a protected species, but I do not think it is in any way convergent towards the Acræas, for it is in no way suggestive of them on the wing, being by no means conspicuous, but rather difficult to follow. Its length of wing has been attributed to relationship with *Acræa*, but this seems open to doubt. I should prefer to consider it as a parallel development to *Acræa*, though it is worth noting that the allied genus *Lachnoenema* has also somewhat elongate wings."

"*Malvern, Oct. 7, 1897.*—The day-flying moths [*Petovia dichroaria*] captured on the same day as *Alena amazoula* can, I think, be well regarded as convergent in coloration."

J. *Mimicry in Lycænidæ and to a less extent in Hesperidæ a Character of the Ethiopian Region. Possible Interpretation.*

The instances of mimicry in South African *Lycænidæ* recorded here, and the much larger number known in other parts of the region, especially the tropical West Coast, led me to inquire how the total number of species of this family compared with that of other parts of the world. My friend Mr. Hamilton Druce kindly made an approximate calculation of the number of described species in the two other great tropical south-extending land masses. From Australia, the Malay Archipelago, and the continental portion of the Oriental Region, over 1000 species have been described. From the Neotropical Region

about 700 species of *Thecla* have been described. In Aurivillius' catalogue of Ethiopian Rhopalocera only 582 species are recognized. The predominance of Lycænid mimicry in this latter Region is therefore in no way connected with richness in the number of species. The chief reason is certainly the existence in the Region of the sub-family *Lipteninæ*, with nearly all its species mimetic. In addition to the general Acraeine appearance of *Alæna amazoula*, the *Neptis*-like *A. nyassæ* and the *chrysippus*-*klugii*-like *Mimacraea marshalli-dohertyi*, there is represented in the Hope Collection mimetic resemblance to *Terias* or other small Pierines on the part of *Larinopoda lireæa*, *L. tera*, *Liptena libyssa*, and *L. undularis*; to *Mylothris* by *Pentila abraxas*, *P. phidia*, and *Citrinophila erastus*; to *chrysippus* and the *chrysippus*-like *Euphadra* and *Aletis* by *Telipna bimaculata* and *T. sanguinea*; to a general Acraeine type by two or three species of *Pentila*. Many other cases of mimicry are known in the sub-family, especially towards models of the genera *Planema* and *Acraea* (see Aurivillius, *loc. cit.*, p. 530). But this remarkable group does not by any means exhaust the Ethiopian Lycænid mimics, for many species of the *Lycæninæ* mimic Acraeas, *Terias* or other small Pierines and *Mylothris*. The general Acraeine mimicry of species of *Catochrysops* has already been described and illustrated. Furthermore, Aurivillius considers that there is a certain amount of mimetic approach between species of *Lipteninæ* and *Lycæninæ* in which the former probably always act as models.

It is very difficult to understand this predominance of Lycænid mimicry in the Ethiopian Region, and I can only suggest the possibility that the number of feasible models of moderate and small size furnished by the abundant Acraeinæ of Africa may furnish an explanation. In such cases as *Catochrysops peculiaris* and *mashuna* we see at once how naturally and easily the Lycænid under-side adapts itself to the characteristic appearance of the *Acraea* type, especially when it is further assisted by similar habits. And this suggests another equally important principle which has doubtless been fertile in bringing about Lycænid mimicry, viz. the habits of the models being such as to bring them within the range of the forms which were to mimic them. The numerous low-flying and low-settling Acraeas, resting at night on grass-stems, have precisely the mode of life which is well known to be characteristic of

such a large number of *Lycanidæ*. The *Lipteninae* are probably a specially-protected group, and the rarity of many of the species may be only apparent, and due to their (Müllerian) mimicry of extremely common forms for which they are constantly mistaken by naturalists.

In other parts of the world *Lycanidæ* which are evidently specially protected and extremely conspicuous are well known, such as *Talicauda* of the Oriental Region and *Eumæus* of the Neotropical. These genera do not enter into synposematic association with the best-defended butterflies of their localities, but each adopts an aposematic appearance peculiar to itself. It is probable that in the Neotropical Region, where mimicry is more striking and more fully exemplified than in any other part of the world, the habits of the *Theclæ* are the chief obstacle to their use of this means of protection. For models of all sizes abound in this part of the world. On the other hand, in the tropical East it may be the want of a sufficient number of models of an appropriate size and habits which has acted as the barrier.

The explanation which has here been thrown out as a suggestion may also enable us to understand the cases of mimicry in Ethiopian *Hesperidæ*, a family in which such resemblances are rare. Here, however, the facts may be paralleled in the Neotropical Region where there are a few mimetic "skippers." Mimicry in this group and the want of it in the *Lycanidæ* may follow from the difference between the habits and stations of the tropical American Hesperids and *Theclæ*.

K. *Mimicry in the Nymphalinae Batesian or Müllerian?*

I have had much controversy with my friend Mr. Marshall over this difficult and interesting problem, and I propose to bring forward a résumé of the arguments which seem to support the latter interpretation as opposed to the former, and then to quote his weighty objections and the interesting observations of the habits of mimetic species and genera which he has made.

1. It is of interest although probably not of extreme importance to reflect that all the great groups of unpalatable, conspicuous, and much-mimicked butterflies belong to the *Nymphalidæ*—the *Ithomiinae*, *Danainæ*, *Heliconinae*, and *Acraina*, and that the two latter are so

closely related to the *Nymphalinxæ* that it is difficult to draw a line between them. The argument is not of much weight, because the intensely procryptic habits and colours of many Nymphaline genera have certainly been brought about by selection due to the great keenness and success of insect-eating animals in their pursuit. I have however suggested and brought evidence in support of the view that some of the procryptic Nymphaline species are to a certain extent unpalatable (see p. 442).

2. Mimicry in the *Nymphalinxæ* does not appear in isolated forms but in all or nearly all the species of a genus. Such mimetic genera are usually very large, dominant, and wide-spread. The species themselves are also often wide-spreading, and may have an enormous range far exceeding that of the model (*Hypolimnas misippus*). Allowing for the fact that the mimetic species resemble the commonest types in the world, and so are liable to escape notice, it is probable that they are rich in individuals. In many instances we know that this is so. The more we investigate it the more does Rhopaloceran mimicry seem to be associated with dominant genera and species, rather than the feeble and hard-pressed forms which H. W. Bates presupposed in his well-known theory.

3. The dominant tendency towards mimetic resemblance in any genus cannot be explained by hereditary transmission of the mimetic form of a single parent species, or from the tendency of closely-related species to vary along nearly the same lines, because the species of a mimetic genus, as a matter of fact, mimic in many different directions. Thus *Pseudacraea* resembles *Acræa*, *Planema*, *Amauris*, and *Limnas chrysippus*; while *Hypolimnas*, including *Euralia*, is even more protean.

4. The non-mimetic species of a mimetic genus are often markedly conspicuous, exhibiting what has all the appearance of an aposematic pattern peculiar to themselves (*Hypolimnas*, *Pseudacraea*). This is also frequently true of the non-mimetic males of a species with mimetic females (*Hypolimnas*). Such aposematic patterns are especially displayed on the under-side, where procryptic colours are developed in other butterflies.

5. The converse of the last argument is also true, viz. some of the species in a genus, which is as a whole markedly conspicuous and itself mimicked, are often mimetic of quite other groups. Many instances of *Neptis*

have been given on pp. 467, 468, and mimetic species are also well known in *Limnitis*, *Uethosia*, etc.

6. The non-mimetic species of mimetic genera are sometimes mimicked; e. g. the mimicry of the *nerina* form of female *Hypolimnias bolina* by a rare Danaine in Celebes, etc. The resemblance of the upper-side of certain species of *Protogoniomorpha* to some of the larger species of *Hypolimnias* may be another instance of the same tendency.

7. The fact that mimetic species resembling some primary model nevertheless in certain respects resemble each other rather than the model. This deuterosynaposematic resemblance, as it may be called, is a very widespread phenomenon, and several striking instances of it are discussed in the present memoir (see pp. 470, 471, 485-7). It will also be shown to occur in Coleoptera (pp. 513-515).

I have given merely an outline of the chief evidence which has induced me to believe that the mimetic Nymphaline genera are to some extent specially protected, and thus have developed a beneficial synaposematic association with far better protected forms belonging to other sub-families.

This evidence has been sought and obtained under the guidance of the principles discovered by Dr. F. A. Dixey and ably presented by him in 1894-97 (Brit. Assoc. Reports, 1894, pp. 692, 693; Trans. Ent. Soc. Lond., 1894, p. 208; 1896, p. 65; 1897, p. 317). These memoirs mark one of the few important advances made in our attempt to understand the complex and difficult phenomena of mimicry. I will quote one pregnant paragraph, which it will be seen contains the essence of what I have here described as primary and secondary mimicry (see pp. 513-515, also the above paragraph 7). "Every conspicuous and distasteful form is a centre of attraction for other forms, whether edible or inedible; but in the former case (Batesian mimicry) the mimetic attraction is limited in operation, and acts only in one direction, influencing nothing but the mimic; while in the latter case (Müllerian mimicry) the mimetic attraction is unlimited and mutual, acting reciprocally in both directions, and influencing each member of the group" (Trans. Ent. Soc. Lond., 1897, pp. 324, 325).

Mr. Marshall's valuable notes on the habits of Nymphaline mimics and his discussion of the conclusions described

above, are contained in the following quotations from his letters.

“*Malvern, Natal; Feb. 21, 1897.*—As regards the *Euralias* my experience of them is somewhat limited, but from what I have seen of them I feel pretty sure that their coloration is due to mimicry and not to convergence. Their range seems in all cases to agree with that of the *Amauris* they resemble. In Durban *A. ochlea* is by far the scarcest of the three, and its mimics *E. deceptor* and *Pseudacraea expansa* are also very rare; further up the East Coast, however (Delagoa Bay and Beira), *ochlea* becomes one of the commonest of the genus, and the two other species are likewise much more numerous. At this place, it is true, *Euralia wahlbergi* is certainly more plentiful than *A. dominicanus*, but they are both uncommon, and all the specimens we see are practically visitors from the thick bush along the immediate coastline. (This is six miles inland.)”

* * * * *

“I may mention that in the last few years Mr. Ball has caught two *Euralia wahlbergi* [in the Karkloof Forest twenty miles N. of Maritzburg], but has never seen *Amauris dominicanus*.”

“*Unkomaas Mouth, Natal; Sept. 3, 1897.*—With regard to the *Euralia*, etc., I must admit that I have never been fully convinced by the contention that in Batesian mimicry the mimetic species must of necessity be a feeble one and very few in numbers. It seems to me that it would be quite reasonable to suppose that such a mimic might well equal or even exceed in numbers the protected species, though this would of course depend entirely upon the degree of inedibility of the latter. For example, in the case of *Euralia mima* and *Amauris echeria* (probably the best-protected butterfly here), supposing they occur in equal numbers in a given area, and that certain birds by chancing to catch three or four of the former in succession were induced to prey upon butterflies with that coloration, then, from a mathematical standpoint, every alternate specimen caught by any bird would be *A. echeria*. Now I think we are quite safe in assuming that the fact that every other butterfly caught had a nauseating taste and smell would be far and away more likely to create a strong and lasting impression upon a bird's mind than the fact that every second one proved to be edible,

and would be quite sufficient to deter the bird from attempting to eat butterflies of that colour. This is from a mathematical point of view solely, but, from what I know of these two forms in life, I believe that presuming them to occur in equal numbers, a larger proportion of *echeria* would actually be captured, for *mima* is a much more shy insect, and although it has the same slow sailing flight (when undisturbed) it does not keep on the wing nearly as long as *echeria*; moreover, it is much more wary and always on the alert for danger, going off at a smart pace when frightened, and not returning to the same spot as *echeria* frequently does after being struck at; altogether it is a much more difficult insect to capture. Indeed I do not see why the mimic should not even somewhat surpass the mimicked species in numbers, without upsetting their relations to one another, provided the taste of the latter be sufficiently unpleasant, and particularly if the flavour be of a *lasting* nature."

"*Malvern, May 14, 1897.*—I feel quite satisfied that *Pseudacraea trimenii* is a mimetic and not a protected species. In spite of its larger size it looks wonderfully like *Acræa acara* on the wing, and the first few examples I caught completely took me in. Their flight is like that of all *Pseudacraeas* and *Euralias*—slow and sailing—so long as they are not disturbed; but if struck at and missed they are off like a shot and do not often give one a second chance. At this particular spot (*Malvern*) they are a good deal commoner than *A. acara*, which is only a rare visitor. The latter is however common on the immediate coast, where *P. trimenii* is I am told pretty plentiful in good seasons."

"*Salisbury, Jan. 12, 1901.*—I quite agree with you that the resemblance between the under-sides of *Delias pandemia* and *Isbarta pandemia* is the most remarkable case yet brought forward, and one cannot but marvel how such exact similarity can have been arrived at. Although I should certainly incline to the belief that the mimicry is Müllerian, judging by the congeners of both forms, yet its very exactitude seems to be a difficulty, for although one can readily understand how in an edible and much-persecuted species the resemblance might be brought up to so high a grade, yet it is hard to understand how this could be effected in a species which is comparatively immune from attack. For it seems to be an inevitable

deduction from the theory of mimicry that a high grade of resemblance must imply excessive persecution, either now or within recent times, unless we are prepared to admit some other convergent force."

"*Salisbury, Sept. 27, 1901.*—With regard to Müllerian mimicry I quite agree that the slow flight and the bright colours of protected forms would lay them open to much experimental tasting from inexperienced birds; but the extreme toughness of their integuments (for example in the *Acraeas*) and their great vitality seem to have been specially developed to minimize this danger. And whereas the Batesian mimic, if thus experimented with, would promptly be eaten, a Müllerian butterfly would run a very good chance of surviving its injuries and propagating its kind. Do not suppose that I in any way disbelieve in the action of Müllerian mimicry, for I certainly think it must be a very strong factor. But this point seems to me to be a real difficulty, and I should like to be able to answer it satisfactorily if it were brought up by an opponent."

L. *Miscellaneous Observations on Mimicry in South African Rhopalocera.* (G. A. K. M.)

a. *Nymphalinae.*

"*Malvern, Natal; Feb. 21, 1897.*—I do not remember ever having seen it suggested that the female of the handsome *Charaxes viphares* mimics *A. echeria*, but I have little doubt that such is the case. It is a fairly common species at the Karkloof, but difficult to catch, and I only took one. I believe there are more instances of mimicry in this genus, e. g. *achæmenes* and *guderiana*, of which the females are very scarce (though the male of the former is one of the commonest *Charaxes* in Mashonaland) and very differently coloured from the males, being remarkably like the common widespread *C. saturnus*. Again, some years ago I pointed out to Trimen the strong resemblance of the female of *C. whytei* to *Neptis agatha* on the wing. I hope to be able to prove before long that *Neptis* is a distasteful genus (by the way, is *Limnitis* edible?), as its appearance and habits certainly point that way."

β. *Picrinæ.*

"*Estcourt, Natal; Oct. 15, 1896.*—In Durban *Mylothris*

agathina was fairly abundant, and I was interested to notice the very close resemblance between it and *Belenois thysa*, though, as is the case with most mimics, the latter has a much quicker flight when disturbed. *B. thysa*, so far as my experience goes, is confined to the warm coast belt, whereas *M. agathina* is common everywhere throughout South-east Africa."

"*Malvern, March 12, 1897.*—It is curious to note that although *Nepheronia argia* was common at the Karkloof, I never saw a single specimen of *Mylothris agathina*. Mr. Ball has in his collection a very fine variety of the female of the former, which clearly mimics *Mylothris trimenia*, the upper-side of the hind-wings being lemon-yellow, and the red mark on the under-side of the fore-wings absent. This is the only one I have seen, although I took one or two females showing an approach towards it, one of which I send you."

"*Umkomwas Mouth, Natal; Sept. 3, 1897.*—I am afraid I can hardly bring myself yet to believe in Dixey's theory that the *Pierinæ* are for the most part protected. As regards our South African species, the only ones which I feel confident are protected are *Mylothris agathina*, *ruppellii*, and *trimenia*, and *Pontia hellica*. For the remainder I think we must find some other cause to account for their numbers and wide range. In *Terias* the larva possesses wonderfully assimilative colouring, and is extremely difficult to detect on the food-plant, and so far as the experience of Hutchinson and myself goes with *T. brigitta* we have never yet observed a single case of parasitism. The protective coloration and comparative freedom from parasites of the larva, and the protective seasonal colouring of the imago, would no doubt go a long way to explain their number, though I fancy there must be some other factor."

"*Salisbury, May 1, 1899.*—Query: are the black bands in the females of *Teracolus* acquired in mimicry of the common and widespread species, *Herpania eriphia*?"*

γ. *Papilioninæ*.

"*Salisbury, Dec. 26, 1897.*—*Papilio brasidas* I consider

* Dr. F. A. Dixey informs me that Professor Westwood probably suspected a relationship between the markings of *H. eriphia* and *T. eris*, for he had removed a specimen of the former species from the others, and placed it next to a dry form of the *Teracolus*.

to be merely a local race of *P. leonidas*, as every one must do who has seen a long series of the two forms. I have found typical *leonidas* pretty plentifully in the low veldt of Mashonaland (Mazoe and Umfuli Rivers) and I also saw it at Delagoa Bay. I have always been struck with its marked difference in habit from the Southern *brasidas*. Its flight is strong and rapid, and it always goes straight ahead like *P. policeses* and *P. antheus*, which it somewhat resembles on the wing in spite of its very different shape. *Brasidas*, on the other hand, has a slow sailing flight, going backwards and forwards over the same ground and often frequenting one spot for days. Now there is absolutely nothing suggestive of protection in the flight of *leonidas*, none of that slow sailing movement to show off its coloration which is so characteristic of the protected *Danainæ* and *Acræinæ*. Moreover, there is no Danaïne occurring south of the Zambesi which is anything like it at all, and this is very significant. I cannot therefore resist the conclusion that in this country *leonidas* is one of those unprotected species which has succeeded in the struggle for existence by its strong rapid flight, and perhaps by protection in the larval stage like *P. demodocus* and *P. corinneus*, whereas in Natal it has found it advantageous, owing to the abundance of *Amauris echeria*, to adapt its coloration in mimicry of that species by the reduction in size and number of the spots in the fore-wing and the toning down of the colour from glaucous green to greenish-white, accompanied by the marked change in its mode of flight. It does not seem to me that convergence would explain the facts, for if *leonidas* is itself protected it should exhibit throughout its range that slow flight which is the 'hall mark' of protection, which it certainly does not in Mashonaland. I believe in Central Africa it is said to mimic *T. petiverana*, and it would be most interesting to find out whether it has there assumed the Danaïne flight."

"*Malvern, Feb. 21, 1897.*—I have been collecting in the Karkloof Forest some twenty miles north of Maritzburg for the last three weeks. The only *Amauris* occurring there is *echeria*, which is very common, though not this year, which is a curiously abnormal one, and as usual the typical female of *Papilio cenea* is common, the *dominicanus*-like form occurring only very rarely. But last year, so my host Mr. Jas. Ball informs me, the latter was very abundant—quite as common as the typical one, and he

caught a long series of them. It seems clear they were not immigrants from Durban, but what caused their appearance in such unusual numbers it is difficult to understand. I may mention that in the last few years Mr. Ball has caught two *E. wahlbergi* but has never seen *dominicanus*. While there, I saw six females of *P. cenea*, two of each of the three forms."

31. WARNING COLOURS AND MIMICRY (ALMOST WHOLLY MÜLLERIAN) IN SOUTH AFRICAN COLEOPTERA. (G. A. K. M., E. B. P.)

[In the groups described below, Coleoptera play a dominant part, either making up the whole or, except in the case of the Mutilloid group, acting as models for other insects. In this one exception the chief interest centres in the Coleoptera, and therefore the group is included here. A certain number of mimetic Coleoptera will be mentioned elsewhere in other groups which have collected round various types of Hymenopterous models.

In the present section the extraordinary predominance of Müllerian associations in South African Coleoptera stands out as the most prominent conclusion.—E. B. P.]

A. Peculiar Warning Patterns and Directive Marks in *Carabidæ* and *Cicindelidæ*. (E. B. P., G. A. K. M.)

Some of the warning patterns of the large *Carabidæ* of the genus *Anthia* are very remarkable and effective, and their development and relationship in the different species extremely interesting.

Six illustrative examples are figured on Plate XVII. In Fig. 21 we see the ancestral appearance, the uniform black of so many large Carabids, in *Anthia massiliata*. Mr. Marshall's account of the habits of the South African members of the genus, printed on page 510, shows that such a beetle is highly conspicuous. It is no doubt an advantage, however, to gain easily-recognizable distinctive marks on the black ground of the exposed dorsal surface, and we find that the species of *Anthia* do, as a rule, possess two or more white patches upon some part of this area. The pair of elongated thoracic white patches, in *A. petersi* (Fig. 22), are borne upon the sides of a thorax which is very like that of *massiliata*, while in *A. thoracica* (Fig. 23) this part of the body is greatly widened and the white patches